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Gestation length variation in domesticated horses and its relation to breed and body size diversity

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Abstract

The domestication process and selective breeding reportedly alter some life history variables. In horses, it has been claimed that gestation length is particularly variable. Some of the factors influencing gestation length are already known and can be grouped into environmental and genetic factors, but the effects of breed and body size have rarely been evaluated. In this study we tested the influence of breed and body size on gestation length for 25 horse breeds from Central Europe. The mean gestation length for all breeds was 342.3 ± 10.2 days and we found significant differences among breeds with a variation of up to 11 days. Body size did not show a significant correlation with gestation length. Our data suggest that breed affiliation explains part of the large variability of gestation length in horses.

Key words: Domestication, life history, *Equus*, evolution

Introduction

The process of domestication can generate changes in animals' life history, including reproductive cycles (Geiger et al., 2016; Herre and Röhrs, 1990). Horses, for example, have a large variation in their gestation length and some researchers suggest that it is even larger than in their wild relatives (Aoki et al., 2013). Full term gestation lengths ranging between 294 and 419 days with viable foals have been described (Rossdale, 1976; West, 1994) but periods considered “normal” range from 300 to 380 days (Aoki et al., 2013; Pérez et al., 2003).

Gestation length is much affected by diverse environmental and individual variables (Meliani et al., 2011). A significantly longer gestation length in mares bred at the beginning of breeding season compared to mares bred at the end of breeding season has been confirmed by various studies (Cilek, 2009; Davies Morel et al., 2002; Dicken et al., 2012; Langlois and Blouin, 2012; Meliani et al., 2011; Pérez et al., 2003; Rezac et al., 2013; Satué et al., 2011; Sevinga et al., 2004; Valera et al., 2006). As it has been found in other species with seasonal activity, e.g. in Przewalski's horses (Bronson and Heideman, 1994; Chen et al., 2008), mares show this foaling accumulation in spring to ensure optimal conditions for the offspring's survival.

Differences in gestation length are also related to the sex of the fetus. It is generally accepted that gestation length has a gender bias in horses and is about 1 to 2 days longer if the mare carries a colt (Aoki et al., 2013; Bene et al., 2014; Cilek, 2009; Heidler et al., 2004; Hintz et al., 1992; Langlois and Blouin, 2012; Marteniuk et al., 1998; Pérez et al., 2003; Sevinga et al., 2004; Staffe, 1935; Taveira and da Mota, 2007; Uppenborn, 1933; Valera et al., 2006; Van Rijssen et al., 2010). This is hypothesized to be caused by testosterone or chromosome linked effects (Cilek, 2009), differences in the interaction with endocrine control of parturition (Jainudeen and Hafez, 2000), or a more developed allantochorion in colts (Wilsher and Allen, 2003). In contrast to the

high number of publications on this subject, two studies could not find differences between male and female foals (El-Wishy et al., 1990; Valente et al., 2006).

Several studies discuss the influence of additional factors such as climate (Mauch, 1937), stud farm where the mares are located during the gestation period (Aoki et al., 2013; Davies Morel et al., 2002; Langlois and Blouin, 2012; Van Rijssen et al., 2010), feeding management (Thorson et al., 2010; Uppenborn, 1933), type of insemination (Bene et al., 2014), inbreeding (Langlois and Blouin, 2012), length of last gestation period (Aoki et al., 2013), interval from ovulation to mating (Davies Morel et al., 2002), unspecified characteristics of the individual mare (Giger et al., 1996; Uppenborn, 1933; Valera et al., 2006; Van Rijssen et al., 2010), reproductive status of the mare (Van Rijssen et al., 2010), parity of the mare (Aoki et al., 2013; El-Wishy et al., 1990; Pool-Anderson et al., 1994; Sanchez, 1998; Staffe, 1935; Valente et al., 2006; Valera et al., 2006; Winter et al., 2007), age of the mare (Aoki et al., 2013; Bene et al., 2014; Bos and Van der Mey, 1980; Cilek, 2009; Davies Morel et al., 2002; Demirci, 1988; Guay et al., 2002; Heidler et al., 2004; Hintz et al., 1992; Kurtz Filho et al., 1997; Langlois and Blouin, 2012; Mauch, 1937; Sevinga et al., 2004; Valera et al., 2006; Winter et al., 2007), unspecified characteristics of the individual stallion (Bene et al., 2014; Mauch, 1937; Van Rijssen et al., 2010), age of the stallion (Davies Morel et al., 2002), artificial light (Caldas et al., 1994; Palmer and Driancourt, 1983), or year of breeding (Cilek, 2009; Langlois and Blouin, 2012; Valera et al., 2006).

Two additional factors are worth considering when examining variation on gestation length: breed and body size. Many of the studies related to gestation length were conducted with a single breed (Caldas et al., 1994; Cilek, 2009; Heidler et al., 2004; Hintz et al., 1992; Howell and Rollins, 1951; Pérez et al., 2003; Rollins and Howell, 1951; Taveira and da Mota, 2007; Van Rijssen et al., 2010; Winter et al., 2007) and results of those including different breeds are contradictory (Bene et al., 2014; Bos and Van der Mey, 1980; Langlois and Blouin, 2012;

Roberts, 1986; Valera et al., 2006). One study showed significant variation of up to six days in the average gestation length among breeds (Bos and Van der Mey, 1980). One review reported differences of up to 13 days among the mean gestation length of different breeds (Satué et al., 2011). The authors argued, however, that the differences among previous reports might not only be caused by breed but also by differences in the way the gestation period was calculated, or differences in climate or photoperiod. On the other hand, no significant differences in gestation length among Hungarian horse breeds were reported by Bene et al. (2014).

Thus, previous studies provide a good overview of factors influencing gestation length regarding individual horse breeds; however, the influence of breed itself and body size remains unclear. In this study, we aim to investigate how those two factors influence the gestation length of the horse. Since research on gestation length of various horse breeds showed significant differences among breeds (Bos and Van der Mey, 1980; Langlois and Blouin, 2012; Valera et al., 2006), we firstly hypothesized that gestation length is a flexible life history variable in horses which does vary among breeds. Secondly, previous research on other domesticated species shows no significant correlation between size and gestation length in different sized breeds (reviewed in Clauss et al., 2014). Thus, we hypothesize that body size does not have a significant influence on gestation length.

Material and Methods

In the present study, we used a total of 30792 gestation lengths (15599 female and 15193 male newborns) from 25 horse breeds (Table 1). All gestation lengths were recorded by studbook societies in Germany and Switzerland (Rheinisches Pferdestammbuch e.V., Schweizer Freiberger Verband) which collected their data in Central Europe. Selected gestation lengths were pregnancies which resulted in one single viable foal during the breeding periods from 2000 to

2015. The duration of a gestation length was determined by the time interval between the last day of mounting/insemination and the day of parturition. Information on the age or parity of the mares was not consistently available in the dataset we collated. We restricted our dataset to gestation lengths ranging from 300 to 380 days due to previous studies referring to a normal gestation length in this range (320 to 360 in Laing and Leech (1975); Rossdale (1976), 300 to 400 in Pérez et al. (2003), 300-380 in Aoki et al. (2013)). In addition, only breeds with a sample size of at least ten individuals were used for the analyses. To visualize the position of wild equids in the allometric linear regression, we added average gestation lengths of four wild equid species from the literature to the figure but did not include them in the statistical analyses (Figure 2).

Previous studies showed that foal gender and month of insemination have a significant influence on the gestation length of horses (see Introduction). Since we aimed to investigate the influence of the breed on gestation length, we calculated a model where the gestation length was linearly adjusted by the influence of foal gender and month of insemination (Linear model: Adjusted gestation length = $a + b \cdot \text{sex} + c_i \cdot \text{month} + \varepsilon$; $a, b, c_i \in \mathbb{R}$; $\varepsilon \sim N(0,1)$; $i \in \{1, \dots, 12\}$). This adjustment is important to isolate the part of the gestation length which is explained by the breed only. We adjusted every recorded gestation length accordingly; in other words, all data presented in this study were adjusted in this manner. In 36 cases, the adjustment led to gestation lengths above the 380 days, which we still included in the following analyses. Differences in gestation lengths among breeds were evaluated using a parametric analysis of variance (ANOVA) followed by a post-hoc Tukey test and a Kolmogorow-Smirnow test of the residuals. To investigate the influence of body size on gestation length in our second analysis, we conducted an allometric linear regression. As a proxy for body size we used mean wither height of each breed according to breeding standards from the literature, since no individual height or weight was indicated in the available data. In contrast to wither height breed standards, no standard body mass data exist

for all the breeds. We correlated the mean wither height to the breed's average gestation length using log-transformed data. The resulting coefficient in the allometric equation is stated, including its 95% confidence intervals in brackets. All statistical analyses were performed using STATISTICA (Version 12, StatSoft Inc., Tulsa, USA) and the significance for all tests was set at $\alpha = 0.05$. Results are displayed as means \pm standard deviation.

Results

The gestation length mean for the 25 breeds was 342.3 ± 10.2 days, with a range between individual animals of 301 – 388 days (Table 1). The ANOVA resulted in significant differences between the 25 breeds ($p < 0.0001$, $F = 13$, for sample size see Table 1) with a maximum mean gestation length of 351 days in Welsh Cobs and a minimum mean gestation length of 340 days in Friesians leading to a variation of 11 days among all means (Figure 1). The post-hoc Tukey tests resulted in 9 out of 300 comparisons which were significant, mainly involving comparisons of Welsh Cobs and Rhenish Warmbloods with other breeds.

Our second analysis, the allometric linear regression, showed no correlation between mean wither height and mean gestation length in our sample (Figure 2). The allometric exponent was low with mean wither height scaling to gestation length^{-0.005} (95% CI: -0.03 to 0.02, $r^2 = 0.007$, $p = 0.67$).

Discussion

Breed affiliation is an important factor influencing variation in gestation length in horses, whereas the effect of body size is not significant. However, parturition time in horses is difficult to predict due to its high variability and unclear indicating signs.

Not all factors which potentially influence gestation length have been examined so far. In this study, we tested the influence of breed and body size on gestation length among 25 breeds.

Differences in calculation of gestation length might introduce some error when comparing studies. Gestation length is often calculated, like in our study, as the period between last mating (or insemination) and parturition. This period, however, is not equivalent to the true gestation length: the period between ovulation and parturition. Galisteo and Perez-Marin (2010) reported that in jennies the difference between true gestation length and gestation length calculated from day of last mating can be around 10 days. In 99.8% of cases, mating occurs before ovulation (Davies Morel et al., 2002). Even after up to a week in the mare's genital tract, sperm is still be able to fertilize (Newcombe, 1994). To determine the day of ovulation, it is necessary to conduct daily examinations using ultrasonic scanning. The difference between the true gestation length and the perceived gestation length thus accounts for some variation among different studies and reviews. Given that we calculated gestation length for all our individuals equally, the variation of our dataset cannot be caused by methodological differences.

Variation in gestation periods could be linked to variation in body size even within breeds; no body size proxy for the individual records was available in our dataset. When comparing between breeds, the breed-specific standard withers height can be considered a valuable proxy that captures differences in body size between breeds reliably; differences between body types (e.g., typically heavily-muscled breeds vs. typically slim breeds) are, however, not represented by this proxy.

In our first hypothesis, we predicted significant differences among breeds, since previous studies on horse breeds showed variation in mean gestation lengths (Bos and Van der Mey, 1980; Langlois and Blouin, 2012; Valera et al., 2006). The results of the ANOVA support our hypothesis by showing significant differences among the 25 horse breeds with a variation of 11 days in mean gestation length. This result agrees with reviewed data from Satué et al. (2011), who listed differences of up to 13 days among mean gestation lengths of different breeds. The

authors, however, argued that differences among various studies in their review might not be caused by breed but by differences in climate, geographical region, or photoperiod. Since we removed photoperiodic effects by calculating a linear model including month of insemination and collected our data in Central Europe, we can reject these variables as having affected our results. We further included foal sex in our linear model to adjust each gestation length accordingly, since previous studies reported foal sex to have a strong influence on gestation length with an increased gestation length in colt pregnancies (see Introduction). As we excluded two of the major influences by adjusting our data, the result of the ANOVA most likely present the variation related to breed affiliation.

Horses are seasonally polyestrous with breeding season starting in spring (McKinnon et al., 2011). Gestation length in seasonal breeders can be influenced by climate and photoperiod. To our knowledge no study exists which shows climate to have a significant influence on gestation length (Aoki et al., 2013; Bene et al., 2014; Bos and Van der Mey, 1980). Photoperiod, however, has been described as the main reason for seasonality (Caldas et al., 1994; Fitzgerald and McManus, 2000) as an increase in daylight hours triggers the transition from anestrus to cyclicity (Palmer and Guillaume, 1992). Various studies showed that artificial light treatment can advance the date of first ovulation after winter anestrus (Palmer and Driancourt, 1983; Scraba and Ginther, 1985). Furthermore, Cilek (2009) reported that gestation length decreases with increasing photoperiod. Hence differences in photoperiod or the application of artificial light at different stud farms might be a reason for variation in gestation length among breeds. All our data have been collected in areas with similar photoperiodic conditions. Thus, we disregard differences in photoperiod as cause for the variation in our dataset.

Including data collected from different stud farms, it is important to acknowledge that differences in management might also account for variation in gestation length. Langlois and Blouin (2012)

found significant differences of ± 1 day in gestation length among French horse breeders which they attribute to varying levels of breeding experience but declared negligible. On the contrary, differences depending on nutrition between war and post-war times of up to 4 days were presented by a different study (Uppenborn, 1933). The influence of nutrition was also confirmed for non-war times by Thorson et al. (2010), who reported differences in gestation length of 6.5 days between mares kept on pastures with or without supplemental grain feed. In our dataset, we cannot account for possible differences caused by management or nutrition, due to the lack of data about the stud farms. Variations in management or nutrition could therefore have an influence on the different breeds and cause some of the variation found in our data.

Another major factor which is still in dispute is the influence of the mare. Some studies state that age of the mare has no significant effect on gestation length (Rezac et al., 2013; Winter et al., 2007), while others report a significant decrease of gestation length with increasing age of the mare. This decrease is supposed to be caused by a decrease in uterine and placental nutritional efficiency or hormonal differences at increasing age (Bos and Van der Mey, 1980; Demirci, 1988; Gluckman and Hanson, 2004; Meliani et al., 2011; Pashen and Allen, 1979). Parity as well as the reproductive states of the mare have been reported as an influence on gestation length by various studies (see Introduction). Furthermore, it has been reported that the mare can regulate the size of the foal (Allen et al., 2002) and suggested that gestation length can be prolonged by the mare by an embryonal diapause between day 20 and 40 (Lofstedt, 1993). The magnitude of the influence of other individual characteristics of mares on gestation length is yet to be determined. Studies on embryo transfer from one breed to another, for example, showed that foals of the larger breed have a lower birth weight than their siblings without embryo transfer if they were carried by the smaller breed and vice versa (Tischner, 1985; Wilsher and Allen, 2003). These differences in birth weight demonstrate that the mare has an influence on the foal. Due to

the high sample sizes of our study, it appears reasonable to suspect that each breed is equally represented by mares of all ages, parities, and reproductive states in our study. Therefore, an influence of the mare as a cause for the variation among breeds in our study appears unlikely, but cannot be ruled out with certainty.

Our dataset included five breeds for which we also found values of mean gestation length in the literature (Table 1). In Arabs, our dataset resulted in a mean gestation length of 342 days and literature results range from 330.42 (Valente et al., 2006) to 340.3 (Valera et al., 2006) days. For Freiburger (341.9 days) only one comparing study could be found with an average gestation length of 336.5 days (Giger et al., 1996). The average gestation length of Friesians (340.5 days) ranges from 331.6 days (Sevinga et al., 2004) to 337.7 days (Bos and Van der Mey, 1980). In Haflinger (341.7 days) values from 337.8 days (Matassino, 1962) to 341.3 days (Bos and Van der Mey, 1980) could be found. Furthermore, the mean gestation length of Shetland ponies (342.1 days) ranges from 333.3 days (Walton and Hammond, 1938) to 337.2 days (Bos and Van der Mey, 1980). In all five cases, the mean gestation length of our study is slightly higher than the highest average stated by literature. This can be explained by the adjustment for sex and season which we included in our dataset.

Reported gestation lengths of wild equids range from around 330 days in Przewalski horses (Maltzan et al., 2007; Monfort et al., 1991) to 425 days in Grevy's zebra (Asa et al., 2001). Thus, reported gestation lengths on domesticated horses showed a larger variation ranging from 294 days (Rossdale, 1976) to 419 days (West, 1994). Although horses show this large variation, the majority of foalings occur between 325 and 368 days (Davies Morel et al., 2002). More data on wild equids are required to understand how domestication affected life history characteristics such as gestation periods in equids.

Our second aim for this study was to investigate the relationship between body size of a breed and its gestation length. Body size is known to account for most of the variability in metabolism (Brown et al., 2004; Speakman, 2005) and some variation in life history traits (Sibly et al., 2012) but does not correlate with gestation length among closely related species or even within species (Clauss et al., 2014). Thus, we hypothesized that gestation length does not correlate significantly with body size. The result of our allometric linear regression supports our hypothesis: it does not show a significant correlation between mean wither height and mean gestation length in horses. It is congruent with studies on other domesticated mammals such as dogs (Kirkwood, 1985), cattle (Andersen and Plum, 1965), and sheep (Bradford et al., 1972), where different sized breeds show similar gestation lengths. As Shetland Ponies (with a wither height of 97 cm) have a birthweight of 13.3% of their adult body weight and Shire Horses (with a wither height of 205 cm) have birth weight of 6.8% of their adult body weight, with both having a similar gestation length (Platt, 1984), it is evident that differences in absolute birth weight are caused by differences in intrauterine growth rate rather than the duration of growth.

Conclusion

Our study showed that the affiliation with breed is one of the factors leading to a large variation in gestation length in horses, whereas body size does not affect gestation length. Parturition in horses is difficult to foresee due to its high variability and unclear indicating signs (Meliani et al., 2011). This causes risks to mare and foal, leading to higher veterinary costs for breeders (Rezac et al., 2013). An increased understanding of the influences on gestation length could help stud farms to decrease the risks associated with foaling and to increase breeding productivity; it could also help to understand the selection pressures that led to potential modifications of gestation length during the process of domestication and breed formation.

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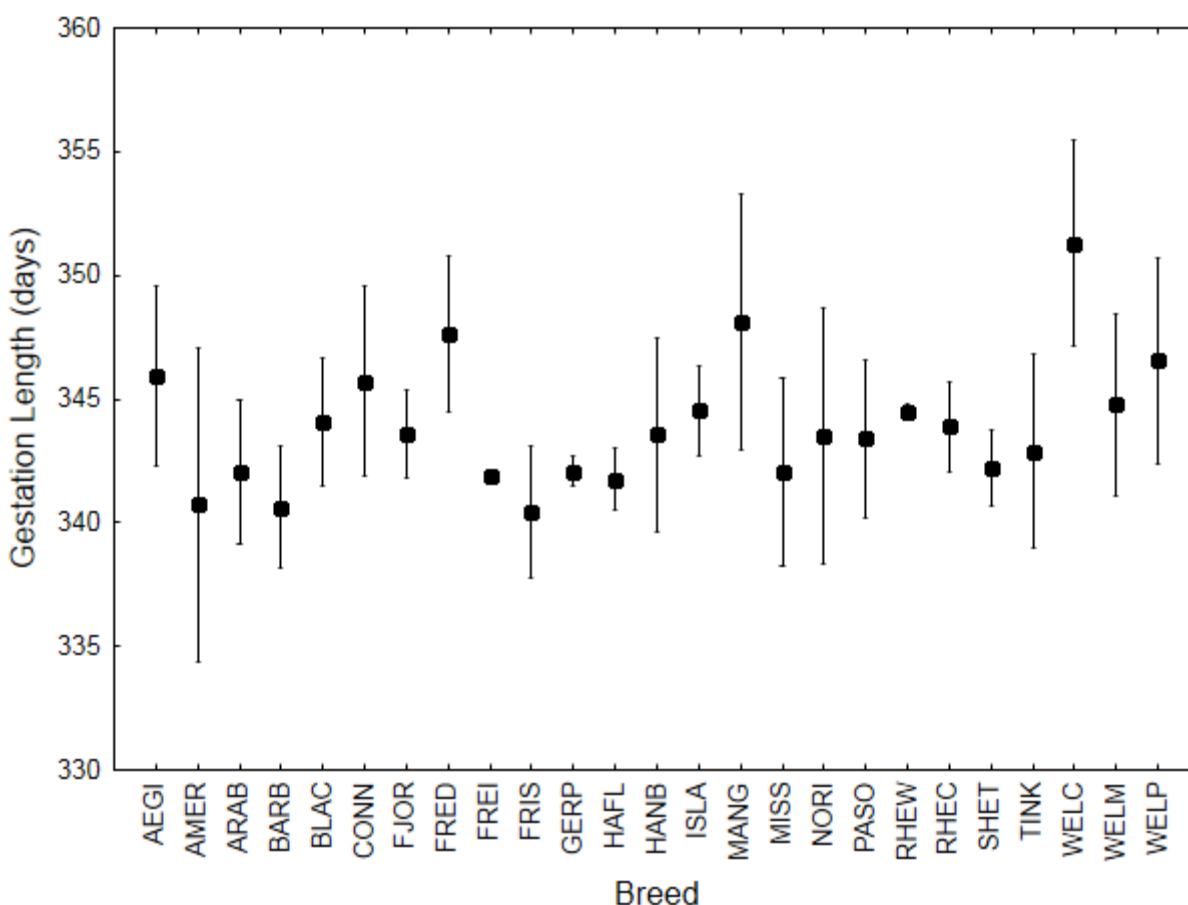
Figure Captions

Fig. 1. Results of the ANOVA for all 25 horse breeds; data on gestation length are adjusted for foal sex and season (see Material and Methods); black squares denote the mean; vertical bars denote the 0.95 confidence intervals; AEGI (Aegidienberger), AMER (American Saddlebred), ARAB (Arab), BARB (Barb), BLAC (Black Forest Coldblood), CONN (Connemara Pony), FJOR (Fjord), FRED (Frederiksborg), FREI (Freiberger), FRIS (Friesian), GERP (German Riding Pony), HAFL (Haflinger), HANB (Haflinger Noble Blood), ISLA (Icelandic Horse), MANG (Mangalarga Marchador), MISS (Missouri Fox Trotter), NORI (Noriker), PASO (Paso Peruano), RHEW (Rhenish Warmblood), RHEC (Rhenish Coldblood), SHET (Shetland Pony), TINK (Tinker), WELC (Welsh Cob), WELM (Welsh Mountain Pony), WELP (Welsh Pony).

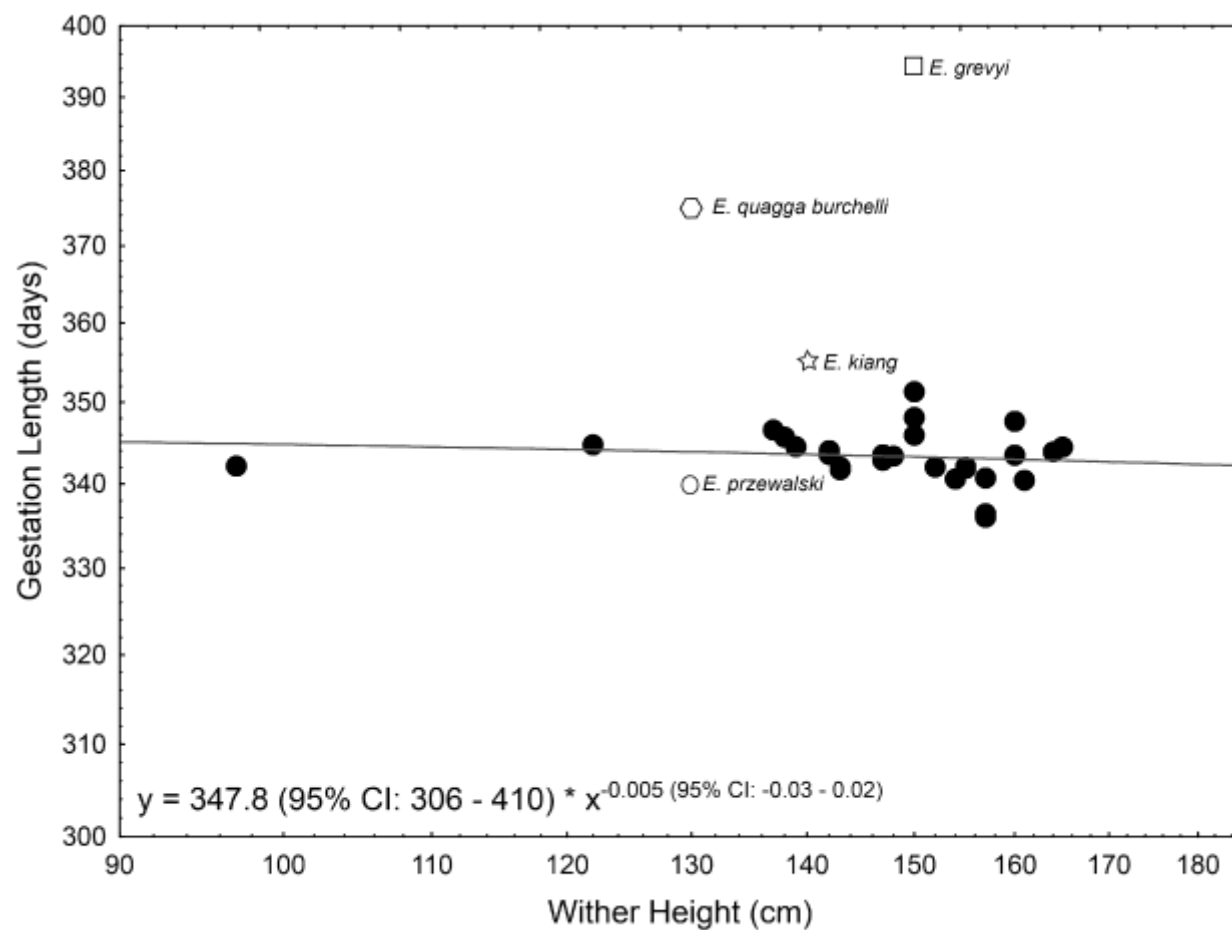


Fig. 2. Correlation of mean wither height and mean gestation length per breed (black circles) in a double log plot; additional data from the literature for wild equids (mean gestation length from different studies, see Table 1, white symbols); a regression line is displayed with the equation printed in the lower left corner.

Table 1

Gestation length in days with standard deviation sorted by breed; additional information on standard deviation, range, and n = sample size; empty cells equals not available.

Authors	Mean	±SD	Range	n _{total}	n _{female}	n _{male}	Breed or Species
This study	345.9	9.2		30	19	11	Aegidienberger
This study	340.7	18.5		10	6	4	American Saddlebred
Valera et al. (2006)	336.8	11.1	290 - 361	532	261	271	Andalusian
This study	342	8.8		48	25	23	Arab
Cilek (2009)	334.3	10.3	332 - 335	2189	1066	1123	Arab
Howell & Rollins (1951)	336.4			186			Arab
Vesovic (1953) ¹	333.7						Arab
Pozo Lora (1954) ⁴	343	11.4					Arab
Demirci (1988) ⁴			314 - 361				Arab
El-Wishy et al. (1990)	332.1	3.3	300 - 371	1570			Arab
Valera et al. (2006)	340.3	9.7	306 - 360	234	129	105	Arab
Meliani et al. (2011)	332.95	8.6		1262	635	627	Arab
Ali et al. (2014)	335.5	10.2	320 - 360				Arab
Valente et al. (2006)	330.42	9.9		147			Arab
Mauch (1937)	338.25	10.2		521	261	260	Arab
This study	340.6	5.9		67	32	35	Barb
Bettini (1955) ¹	333.8						Belgian
Becze (1958) ¹	336.5						Belgian
This study	344	9.3		60	28	32	Black Forest Coldblood
Hrasnika (1944) ¹	339.1	0.9					Bosnian Pony
Satué (2004) ⁴	332.4		297 - 358	44			Carthusian
Pérez et al. (1997) ⁴			322 - 359	38			Carthusian Spanishbred
Pérez et al. (2003)	338.95	9.6	319 - 359	364			Carthusian Spanishbred
This study	345.7	9.8		27	14	13	Connemara Pony
Winter et al. (2007)	335.6	10.5	312 - 364	70			Criollo
Rezac et al. (2013)	339.2	11.3	305 - 392	321	165	156	Czech Warmblood
Bos and van der Mey (1980)	343.3			2002	1242	760	Draught Horse

This study	343.5	10.2		127	63	64	Fjord
This study	347.6	12.2		40	23	17	Frederiksborg
This study	341.9	10		23700	12060	11640	Freiberger
Giger et al. (1997) ⁴	336.5		307 - 361	193			Freiberger
This study	340.5	11.3		56	31	25	Friesian
Sevinga et al. (2004)	331.6			495			Friesian
Bos and van der Mey (1980)	337.7			426	236	190	Friesian
Bene et al. (2014)	334.3	12.9		47			Furioso - North Star
This study	342	10.7		1080	549	531	German Riding Pony
Mauch (1937)	336.29	11.2		424	224	200	Gidran
This study	341.7	7.5		264	130	134	Haflinger
Matassino (1962) ⁴	337.8	13					Haflinger
Bos and van der Mey (1980)	341.3			1034	593	441	Haflinger
This study	343.5	7.9		26	16	10	Haflinger (Noble Blood)
Bene et al. (2014)	335.2	14.9		122			Hungarian Cold Blooded
Bene et al. (2014)	333.6	19.8		146			Hungarian Sport Horse
This study	344.5	9.9		122	64	58	Islandic Horse
Bene et al. (2014)	336.2	14.8		123			Kisberi
Ilancic (1958) ¹	333.5						Lipizzaner
Heidler et al. (2004)	334.3	7.3		46	24	22	Lipizzaner
Bene et al. (2014)	334	9.8		60			Lipizzaner
Mauch (1937)	333.88	9.3		252	130	122	Lipizzaner
This study	348.1	13		15	8	7	Mangalarga Marchador
This study	342	8.7		28	13	15	Missouri Fox Trotter
Hura et al. (1997) ⁴	332.4	6.9		298			Nonius
Bene et al. (2014)	335.1	15.3		146			Nonius
Mauch (1937)	335.92	10.4		432	207	225	Nonius
This study	343.5	10.5		15	7	8	Noriker
This study	343.4	10.2		39	14	25	Paso Peruano
Bettini (1955) ¹	342.2						Percheron
Aoki et al. (2013)	334.9	8.3	313 - 352	209	103	106	Percheron Mix

Zwolinski(1964) ⁴			299 - 375				Polish
Pool-Anderson et al. (1994)	343/333			12			Quarter Horse
Guay et al. (2002)			339 - 344	12			Quarter Horse
Duggan et al. (2008) ⁴			317 - 375	26			Quarter Horse
This study	344.5	10.6		4647	2305	2342	Rhenisch Warmblood
This study	343.9	11.7		122	59	63	Rhenish German Coldblood
Salerno and Montemurro (1966)	340.9	8.7					Salernitan
Bene et al. (2014)	333.3	12.7		36			Shagya
Walton & Hammod (1938)	333.3		323 - 343	3			Shetland
Bos & van der Mey (1980)	337.2			2327	1520	807	Shetland
First & Alm (1977)	334.4	3.17	322 - 344	7			Shetland
This study	342.1	14.5		168	74	94	Shetland
Pozo Lora (1954) ⁴	343.6	12.2					Spanishbred
Blesa (1999) ⁴			322 - 346				Spanishbred
Pundir (2004)	333		308 - 365	36			Spiti
Villani & Romano (2008)	337	7		350			Standardbred
Marteniuk et al. (1998) ⁴			302 - 383	296			Standardbred
Dicken et al. (2012)	349	9.3	303 - 384	614 ⁵	313	295	Standardbred
Evans (2010)	349		312 - 393	1109	553	556	Standardbred
Tischner (1985)	325			2			Tarpan
Detkens (1953) ¹	338.8						Thoroughbred
Hintz et al. (1992) ⁴			319 - 364				Thoroughbred
Allen et al. (2004) ⁴			325 - 339	14			Thoroughbred
Duggan et al. (2008) ⁴			322 - 366	18			Thoroughbred
Kurtz Filho et al. (1997)	334		315 - 360	390			Thoroughbred
Davies Morel et al. (2002)	344.1	0.5	315 - 388	433	238	195	Thoroughbred
Sanchez (1998) ²	341.3	10.1	306 - 381	5472			Thoroughbred
Taveira & da Mota (2007)	337.83	9.5	302 - 396	25477	12927	12550	Thoroughbred
Elliott et al. (2009)			321 - 360	348	178	170	Thoroughbred
van Rijssen et al. (2010)	352	10	309 - 398	627			Thoroughbred
This study	342.8	10.9		26	18	8	Tinker

This study	351.3	14.8		23	12	11	Welsh Cob
This study	344.7	8.6		29	19	10	Welsh Mountain Pony
This study	346.5	12.6		23	10	13	Welsh Pony
Pagan et al. (2009)			377 - 404				<i>Equus africanus somalicus</i>
Monfort et al. (1991)	340.2	6.8	331 - 352	6			<i>Equus ferus przewalskii</i>
King (1965)	399						<i>Equus grevyi</i>
Read et al. (1988) ³	390						<i>Equus grevyi</i>
Asa et al. (2001)	407.3		391 - 425	3			<i>Equus grevyi</i>
King (1965)	371						<i>Equus quagga boehmi</i>
Wackernagel (1965)	371.2		361 - 390	28			<i>Equus quagga boehmi</i>
Brown (1936)	347		340 - 354	2			<i>Equus quagga burchellii</i>
Klingel (1969) ³	381.5		378 - 385				<i>Equus quagga burchellii</i>
Smuts (1976)	396			1			<i>Equus quagga burchellii</i>
Joubert (1974) ³	362						<i>Equus zebra hartmannae</i>
Penzhorn (1985)	359						<i>Equus zebra zebra</i>

¹cited in Salerno and Montemurro (1966), ²cited in Perez et al. (2003), ³cited Nuñez et al. (2011), ⁴cited in Satué et al. (2011), ⁵sex recorded for 608 individuals